Marine Environmental Research 148 (2019) 1–11

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Climate change induced range shifts in seaweeds distributions in Europe

Camino Fernández de la Hoz, Elvira Ramos, Araceli Puente, José A. Juanes*

Environmental Hydraulics Institute, Universidad de Cantabria - Avda. Isabel Torres, 15, PCTCAN, 39011, Santander, Spain

ARTICLE INFO

Keywords:
Algae
Ecological niche
Global change
Marine ecology
Physiological thresholds
Species distribution models

ABSTRACT

There are evidences of how climate change is affecting seaweeds distribution and the ecosystems services they provide. Therefore, it is necessary to consider these impacts when managing marine areas. One of the most applied tools in recent years to deal with this are species distribution models, however there are still some challenges to solve, such as the inclusion of hydrodynamic predictors and the application of effective, transferable and user-oriented methodologies.

Five species (*Saccorhiza polyschides*, *Gelidium spinosum*, *Sargassum muticum*, *Pelvetia canaliculata* and *Cystoseira baccata*) in Europe and 15 variables were considered. Nine of them were projected to the RCPs 4.5 and 8.5 for the mid-term (2040–2069) and the long term (2070–2099). Algorithms for each species were applied to generate models that were assessed by comparison of probabilities and observations (area under the curve, true skill statistics, Boyce index, sensitivity, correct classification rate), niches overlap (Schoener's D, Hellinger's I), geographical similarity (interquartile range) and ecological realism.

Models built demonstrated very good predictive accuracy and sensitivity, without overfitting risk. A medium overlap in the historical and RCPs environmental conditions were obtained, therefore the models can be considered transferable and results accurate because only some isolated points were detected as outliers, corresponding to low probabilities.

The areas of *S. polyschides* and *G. spinosum* have been identified to be dramatically reduced, meanwhile *S. muticum* and *C. baccata* were predicted to expand their range. *P. canaliculata* was expected to keep its sites of presence but with a decrease in its probability of occurrence. For all species it was remarkable the importance of hydrodynamic variables and parameters representing extreme conditions. Spatially predictions of the potential species and areas at risk are decisive for defining management strategies and resource allocation. The performance and usefulness of the approach applied in this study have been demonstrated for algae with different ecological requirements (from upper littoral to subtidal) and distributional patterns (native and invasive), therefore results can be used by marine planners with different goals: marine protected areas designation, monitoring efforts guiding, invasions risk assessment or aquaculture facilities zonation.

1. Introduction

There are evidences of how climate change is affecting marine communities and consequently, the ecosystem services they provide (Cheminée et al., 2013; Doney et al., 2012; Liquete et al., 2016). Among marine flora, seaweeds dominate intertidal and subtidal environments (Lüning et al., 1990). Their role as engineering species defines the structure and functioning of the benthic assemblages through biotic and non-biotic interactions (Schiel, 2006). Therefore, a comprehensive understanding of consequences of climate change in their distributional patterns is a core requirement for adopting an ecosystem-based management (Sax et al., 2013), such as resources management, establishment of marine protected areas or measures to face invasions (Duarte et al., 2017; Tamburello et al., 2014). To reach this objective it is required the identification of the variables and parameters that determine species ecology (Araújo et al., 2019) and the definition of their physiological thresholds. When working in large areas, hydrological variables (e.g. wave height, current speed or bottom and wind stress) are usually not considered, although there is evidence of their relevance in species distribution (de la Hoz et al., 2018b; Pace et al., 2017; Ramos et al., 2014). Likewise, the formulation of biologically-meaningful parameters is essential to get realistic models, but abiotic information availability is usually limited to general parameters, not taking into account for example extreme events (although see Cavole et al. (2016); Hughes et al. (2017); Marshall et al. (2013); Smale and Wernberg (2013)), whose importance in climate change context will be decisive

* Corresponding author.
E-mail addresses: camino.fernandez@unican.es (C.F. de la Hoz), ramose@unican.es (E. Ramos), puentea@unican.es (A. Puente), juanesj@unican.es (J.A. Juanes).

https://doi.org/10.1016/j.marenvres.2019.04.012
Received 11 January 2019; Received in revised form 17 April 2019; Accepted 29 April 2019
Available online 30 April 2019
0141-1136/ © 2019 Elsevier Ltd. All rights reserved.

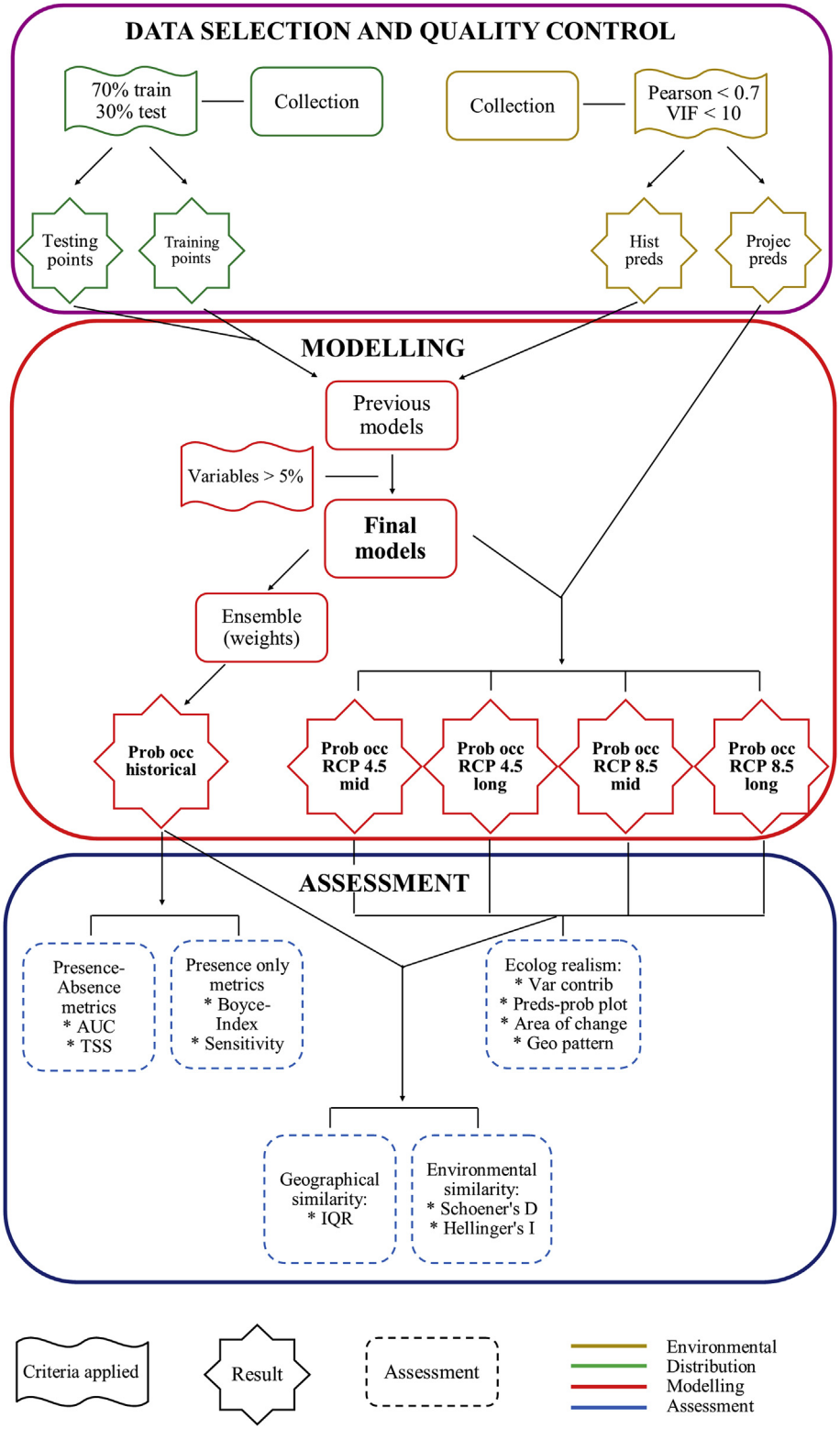

Fig. 1. Process followed in this work. Wave rectangles represent the criteria applied, stars the results and dashed rectangle the assessment techniques. VIF, variance inflation factor; Prob occ, Probability of occurrence; Proj; projection; AUC, area under the receiver–operating curve; TSS, true skill statistic; IQR, Interquartile range.

(Lima and Wethey, 2012; Oliver et al., 2018; Seabra et al., 2015). Concerning species tolerance thresholds, experimentation provides valuable information (Celis-Pla et al., 2017; Martínez et al., 2012) but extrapolation from laboratory to field conditions can be tricky. One of the most applied tools to deal with this are Species Distribution Models (SDMs), whose applications in recent years have increased significantly because they map efficiently large areas where field-collected data are limited or unavailable (Álvarez-Martínez et al., 2018). They are based on a quantification of species-environment relationships by using numerical tools (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000). Nevertheless, their implementation in decision-support systems is sometimes limited due to managers' difficulty to develop them.

The objective of this work is to provide an overview of climate change driven range shifts of representative seaweeds in Europe. Besides, dependence plots are expected to be generated to improve the knowledge of species physiological thresholds in a cost-effective way.

2. Material and methods

The methodology presented in this work is divided into three main steps (Fig. 1):

1) Data selection and quality control. Predictors related to seaweed ecology (environmental data) and biological records of five macroalgae (distribution data) were collected from 1985 to 2015.
2) Modelling. The best algorithms for each species were selected and their settings adjusted by including only the most explanatory predictors (with a contribution higher than 5%).
3) Assessment. Model performance metrics were calculated and models assessed in the environmental and geographic space. Besides the ecological realism of results was tested.

2.1. Study area

The study was focused on all European seas, at two different resolutions: 0.1° for coast (until 50 m depth) and 0.5° for oceanic waters. The final mesh had 18200 points (12074 coastal and 6126 offshore) (de la Hoz et al., 2018a).

2.2. Distribution data

Five species were considered in this study: *Saccorhiza polyschides*, *Gelidium spinosum*, *Sargassum muticum*, *Pelvetia canaliculata* and *Cystoseira baccata*. They were selected as representative of 21 seaweeds (Table A1. Appendix A. Supplementary material) defined by grouping them according to their ecological requirements, through a Self-Organizing Maps and component-planes analysis (Kohonen, 1998; Vesanto, 1999).

Biological records were collected from 1985 to 2015 from the sources of Table A2 Appendix A Supplementary material. Only records with geographic information was considered. Besides, all presences were checked by experts to remove possible geographic errors. Occurrences were gridded and only one per cell was considered. Representative training points were selected (70%), using 30% of data for testing (Fig. 2).

Pseudo-absences were randomly generated in the geographic space (1000 points), not overlapping presence sites (Barbet-Massin et al., 2012; Guisan et al., 2017; Phillips and Dudík, 2008), with the R package *sdm* (Naimi and Araujo, 2016).

2.3. Environmental data

Abiotic variables were collected from OCLE database (de la Hoz et al., 2018a) for each mesh point. For the historical period (1985–2015) 15 variables were considered: sea surface temperature (SST), significant wave height (Hs), salinity (Sal), air temperature (AT), wind speed (Ws), tidal range (TR), bottom shear stress (Tmax), bottom orbital speed (Urms), currents (Uw), radiation (Rss), light attenuation coefficient (Kd), pH (pH), nitrate (Nit), bathymetry (bathy), substrate (sub, categorised in mud, sand, coarse substrate, mixed sediment and rock). Nine variables were projected to the Representative Concentration Pathways (RCPs) 4.5 and 8.5 (IPCC, 2014) for the mid-term (2040–2069) and the long term (2070–2099): SST, Hs, Sal, AT, Ws, Rss, pH, Nit, Sea Level Rise (SLR). Units and periods of raw data can be consulted in Table A3 Appendix A. Supplementary material. For each variable, a complete set of parameters was considered: maximum (max), minimum (min), mean (mean), standard deviation (std), range (rg) and percentiles (P) 10^{th}, 25^{th}, 50^{th}, 75^{th} and 90^{th}. Additionally, to detect changes in extreme conditions for SST and AT the number of consecutive days that the percentile 90^{th} is exceeded (Torresan et al., 2016) and for Tm the number of days over 2.2 Nt/m^2 (Vousdoukas et al., 2012) (Days) were calculated. Furthermore, for projections, the same parameters were calculated seasonally, yearly and for the full period.

Collinearity of parameters was tested for the 642 parameters with the criteria of Pearson correlation coefficient < 0.7 and variance inflation factor (VIF) < 10 in the points with species presence (predictors correlation Table A.4 Appendix A. Supplementary material), using the R package *usdm* (Naimi et al., 2014). VIF (Montgomery and Peck, 1982) values from five to ten are considered as critical for multivariable correlation (Guisan et al., 2017). Non-correlated predictors for each species can be consulted in Table A.5 Appendix A. Supplementary material.

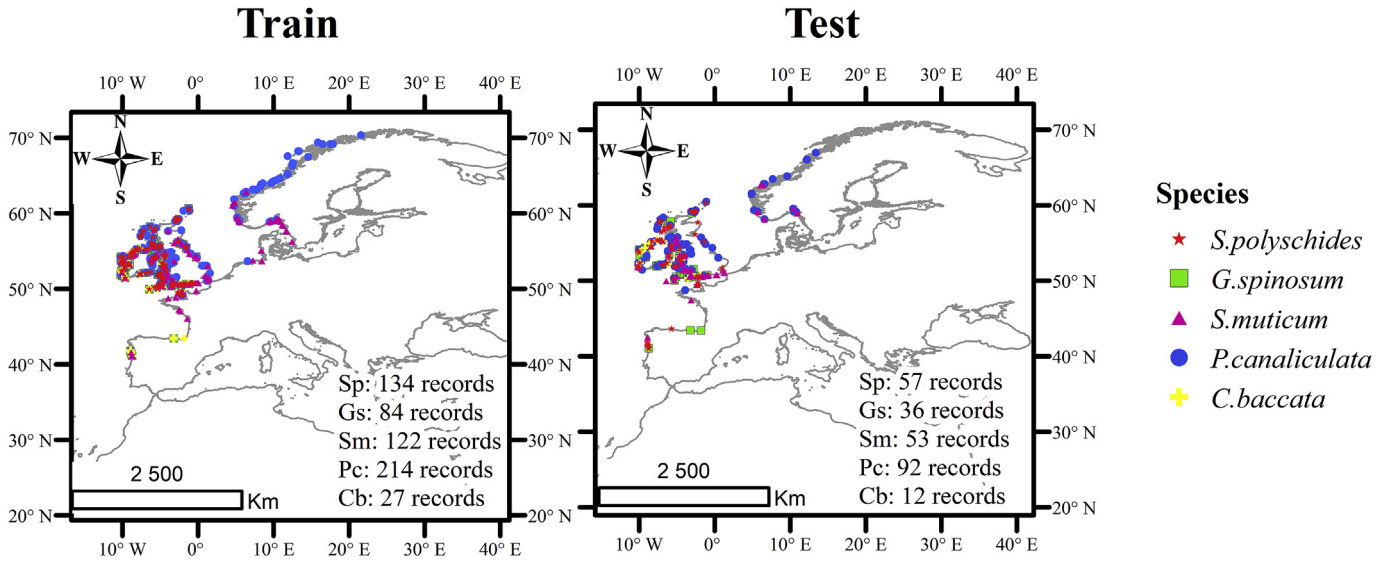

Fig. 2. Presences records used for training and testing. Sb, *Saccorhiza polyschides*; Gs, *Gelidium spinosum*; Sm, *Sargassum muticum*; Pc, *Pelvetia canaliculata*; Cb, *Cystoseira baccata*.

Table 1
Algorithms and weights applied for each species.

SPECIES	ALGORITHM	WEIGHT
S. polyschides	RF	70.91
	CART	29.09
G. spinosum	GLM	26.04
	GAM	21.88
	RF	21.88
	MAXENT	22.92
	MDA	7.29
S. muticum	RF	44.83
	MAXENT	55.17
P. canaliculata	GLM	7
	RF	25.5
	MAXENT	40
	MDA	27.5
C. baccata	RF	85.72
	MAXENT	14.29

2.4. Modelling

Nine correlative algorithms were ran (Generalized Linear Model (GLM (McCullagh and Nelder, 1989)), Generalized Additive Model (GAM (Hastie and Tibshirani, 1990)), Multivariate Adaptive Regression Spline (MARS (Friedman, 1991)), Mixture Discriminant Analysis (MDA (Hastie et al., 1994)), Classification and Regression Trees (CART (Breiman, 1984)), Support Vector Machine (SVM (Vapnik, 1995)), Flexible Discriminant Analysis (FDA (Hastie et al., 1994)), Random Forest (RF (Breiman, 2001)) and MAXENT (Phillips et al., 2006)) in two independent periods to test their temporal transferability. For each species, environmental and distribution data were split into two independent periods (P1: 1985–1996 and P2: 2004–2015) and their sensitivity and temporal transferability tested through Tuanmu equations (Tuanmu et al., 2011). Therefore, the best algorithms and their weights in the ensemble procedure were defined for each species to ensure the ability of the final models to be transferred to other times.

A preliminary model was built with all non-correlated predictors and those with a contribution higher than 5% were included in the final models (Coro et al., 2015). New models were ran with the selected predictors and the same training and testing points and projected into the historical and climate change conditions. An ensemble (Araujo and New, 2007) was built for each species by averaging the results of the algorithms according to weights (Fig. 1).

The models were built, evaluated and projected using the *sdm* package (Naimi and Araujo, 2016).

2.5. Assessment

Models were assessed considering different metrics to provide information about their predictive power (Fig. 1). First, predicted probabilities of presence versus presence-absence observations were calculated, through the area under the receiver–operating characteristic curve (AUC (Hanley and McNeil, 1982)) and the true skill statistic (TSS (Allouche et al., 2006)). AUC varies from 0.5 for a model whose predictions are no better than random, to 1 for perfect agreement with the observed data. TSS varies between 0 (random model) and 1 (perfect agreement). Models with AUC > 0.9 were considered "very good", in the range 0.7–0.9 "reasonable predictions", and values < 0.7 "poorly accurate" (Araújo and Pearson, 2005; Swets, 1988). For TSS the predictive power of models were classified as "poor" for values < 0.4, "good" in the range 0.4–0.8 and "excellent" from 0.8 to 1 (Allouche et al., 2006; Zhang et al., 2015). Analysis of AUC and TSS were performed in R, using the *pROC* (Robin et al., 2011) and *sdm* (Naimi and Araujo, 2016) packages, respectively. Additionally, model overfitting was calculated as the difference between training and testing AUC, with higher values indicating over-parameterizing (Jiménez-Alfaro et al., 2018; Warren and Seifert, 2010).

Probabilistic predictions were compared to presence-only observations with the Boyce index (Boyce et al., 2002). Besides, as the goal of the study was to detect species and their areas at risk in climate change scenarios, sensitive models were desired, therefore the correct classification rate (CCR) was used as threshold to define presences.

As different abiotic combinations exist between the historical and projected scenarios, niche overlap was tested on the environmental conditions and on the geographical area. In the first case, the assessment was conducted through Schoener's D (Schoener, 1989) and modified Hellinger's I metrics (Warren et al., 2008) with the PCA-env ordination in the R package *ecospat* (Broennimann et al., 2016). They range from 0 (no overlap) to 1 (identical niches), values higher than 0.6 are considered as high overlap (Broennimann et al., 2012). On the other hand, the geographical similarity was assessed through the interquartile range (IQR) (Acuna and Rodriguez, 2004; Pérez et al., 2014) to detect the areas where the climate is non-analogous, therefore predictions in those areas have to be considered carefully. IQR was calculated in each point of the mesh for historical and projected maps and values lower than Q1-1.5(IQR) and higher than Q3 + 1.5(IQR) were considered as outliers.

Concerning the ecological realism of models output, different analyses were conducted in R (R Core Team, 2018). For each species the contribution of predictors to model were obtained by averaging the algorithms results according to weights (Table 1). Besides, the fitted model of each species was applied separately for each predictor to get the physiological thresholds. Additionally, the relative area of change between periods was calculated after reclassifying the output using CCR as threshold. Additionally to mathematical assessment, results were also visually evaluated.

3. Results

3.1. Assessment metrics

Final models' goodness-of-fit and discrimination performance could be considered very good according to AUC and TSS, with values over 0.93 and 0.84 respectively (Table 2). Presence-only metric Boyce-Index showed close to perfect predictions, with values over 0.91 in all cases. Boyce index plots are represented in Fig. A.6 Appendix A. Supplementary material. Sensitivity can also be considered good for all species, with more that 60% of presences well predicted, except in the case of *P. canaliculata* because of the high value of the CCR used as threshold (0.74) (Table 2). The difference between training and testing AUC (AUC_{diff}) showed low values for all species, indicating that the risk

Table 2
Summary of the assessment metrics by species.

	S. polyschides	*G. spinosum*	*S. muticum*	*P. canaliculata*	*C. baccata*
AUC	0.93	0.98	0.99	0.97	0.98
TSS	0.84	0.93	0.93	0.86	0.94
BOYCE INDEX	0.99	0.94	0.99	0.99	0.91
CCR	0.43	0.35	0.11	0.74	0.31
SENSITIVITY	73.30	61.67	100	11.44	69.23
AUC_{diff}	0.039	0.007	0.004	0.0002	0.019

Table 3
Overlap values for the RCPs considered.

	RCP 45m	RCP 45l	RCP 85m	RCP 85l
Schoener's D	0.45	0.40	0.39	0.29
Hellinger's I	0.71	0.63	0.61	0.56

that models were over-parametrized was small (Russo et al., 2014; Warren and Seifert, 2010).

Niche overlaps comparison showed that abiotic environments were more different for the RCP 8.5 than for RCP 4.5 and for long term than mid-term, showing a clear gradation in both metrics (Table 3). According to Fig. A.7 Appendix A. Supplementary material, a medium overlap can be considered in general, although it decreased in the RCP 8.5 and the long term (Broennimann et al., 2012).

3.2. Ecological realism

Concerning predictors contribution (Fig. 3), it was remarkable the importance of hydrodynamic variables, such as Tm, Uw, Urms or Hs, present in all models. Besides, SST also contributed in all models except in *P. canaliculata*'s. Desiccation variables, as AT or Ws, were also important for all species, except for *S. polyschides*. Variables such as Kd, pH, bathymetry, substrate or Rss were important for all species with different percentage. Concerning parameters, extreme and variability indicators were the most represented. Numerical value of predictors contribution can be checked in Table A.5 Appendix A. Supplementary material. Note that substrate categories were represented by numbers, being 1 mud, 2 sand, 3 coarse, 4 mixed and 5 rocky.

Dependence plots (Figs. A.8-A.12 Appendix A. Supplementary material) showed species physiological thresholds for each predictor, such as the high probabilities in semi-exposed rocky shores and high intertidal of *P. canaliculata*, sheltered areas in the case of *C. baccata* and hard substrates for *S. muticum*. Besides species' tolerance to predictors is clearly defined by the different probabilities of presence. For example, it is exposed *S. muticum*'s tolerance to high values of currents and temperatures and low variability in nitrate.

According to the predicted geographical distribution of species, Fig. 4 showed the difference in the probability of occurrence species between RCPs and historical predictions. In addition, all RCPs and periods were represented in Figs. A.13-A.17 Appendix A. Supplementary material with different scales to allow a better visualization. Visual assessment showed that for *S. polyschides* and *G. spinosum* a remarkable decrease in habitat suitability was predicted in the whole distribution area, reaching values lower than 0.2 in the RCP 8.5 long term. *S. muticum* southern areas reduce their suitability, until disappear in the Iberian Peninsula; meanwhile probability increase in northern areas. *P. canaliculata* probabilities of occurrence in the west of Britain might decrease slightly, whereas the suitability of some areas around the Brittany and the English Channel increase. The suitable habitat for *C. baccata* was predicted to increase in all RCPs around UK and the Gulf of Biscay. Only some isolated points were detected as outliers in the IQR assessment (Fig. A.18 Appendix A. Supplementary material), which usually correspond to low probabilities, therefore results can be considered accurate.

4. Discussion

Models developed in this work predicted, with good performance, important changes in the habitat suitability of the five seaweeds considered. Results can be transferable to 21 species and broadly applied in Europe, becoming a very useful management tool in wide-ranging climate change studies in the marine environment. One of the main contributions of this work is the inclusion of the most complete set of parameters in seaweeds assessment until now (de la Hoz et al., 2018a), which improves the existing knowledge in inferring the environmental forces shaping their distributions, and the selection of algorithms and their weights according to their temporal transferability (Regos et al., 2019).

Despite not being usually considered in SDMs, this study reinforces previous findings about the importance of hydrodynamic variables in marine flora distribution (de la Hoz et al., 2018b; Jonsson et al., 2018; Ramos et al., 2014). Besides, the relevance of widely used variables, such as SST was also confirmed (Bosch et al., 2017; Martínez et al., 2018; Piñeiro-Corbeira et al., 2018). Results remark the decisive role of extreme conditions in seaweeds distribution, supporting the importance of considering stressful parameters (Assis et al., 2017; Galván et al., 2016; Vranken et al., 2018). Previous studies have already established the importance of SST for *S. polyschides* (Fernandez, 2011; Norton, 1977), especially focused on their maximum during growing season. Additionally this work remarks the importance of variability (Werner et al., 2016), reason why it was reported to survive only in areas with narrow temperature range (Lüning et al., 1990). *S. polyschides* lives in the subtidal (Assis et al., 2013), but often extends on to the lower shore, which explained the importance of TR as a limiting factor. The model selected also nitrate availability as a critical factor of *S. polyschides* growth. The importance of Tm minimum in fall shows its preference for areas of low energy, although it is able to tolerate strong currents (Norton, 1978). Concerning its geographical distribution, for the historical period it was confined to the coasts of UK and the Brittany, in agreement with current knowledge (Burrows et al., 2018). However, the model did not identify the records in the north and west coast of the Iberian Peninsula reported by other authors (Assis et al., 2013; Fernandez, 2011). This can be the consequence of the scarcity of data in this area during the training process, which could have excluded some environmental combination important for the area. Projections agreed with previous studies that suggest their practically disappearance, especially towards the southern edge (Araújo et al., 2016; Assis et al., 2018). Meanwhile other authors, such as Assis et al. (2018), detects the northward migration of *S. polyschides* in the RCP 8.5, our results suggest an important disappearance in the following decades, although some migration in depth would happen for the populations situated below the summer thermocline (Assis et al., 2016) because low probabilities remained in UK and Brittany. This quick range shift was in the line of the field observations carried out in the north of Spain, where after 30 years populations had shorter generations and a smaller fraction becomes reproductive (Fernandez, 2011).

The link of *G. spinosum* with SST has been studied (Rueness and Fredriksen, 1989), however its variability is usually not considered despite its importance according to this work. Besides, results showed the importance of extreme SST, with the inclusion in the model of the Days parameter, whose high values decreased *G. spinosum* probability of occurrence. This lethal effect of high temperatures has been already reported (Fralick et al., 1990), however the consecutive effect has not been considered until now. Light is an important factor to *G. spinosum* (Fralick et al., 1990; Rico, 1992), especially its range in extreme seasons, winter and summer. Its historical distribution presented higher probabilities of occurrence in the north populations (Ireland and west of UK) than in southern ones (Brittany and Iberian Peninsula). Models predictions suggested an extinction of the species under both RCPs considered, even in the mid-term. This trend toward decline has already been observed in its biomass between 1985 and 2002 (Sánchez et al., 2005). These authors suggest a competition for light, which could be softened in climate change scenarios. However, for other *Gelidium* species high light stress triggers photobiological changes that could involve photoinhibition (Quintano et al., 2019).

The most important parameter for *S. muticum* was Uw_P75, according to the studies that establish its high tolerance to currents, even at extreme conditions (Josefsson and Jansson, 2011). As it has to deal with desiccation, variables such as TR, Ws or AT were also included in the model. It was also remarkable the importance of the Days parameter

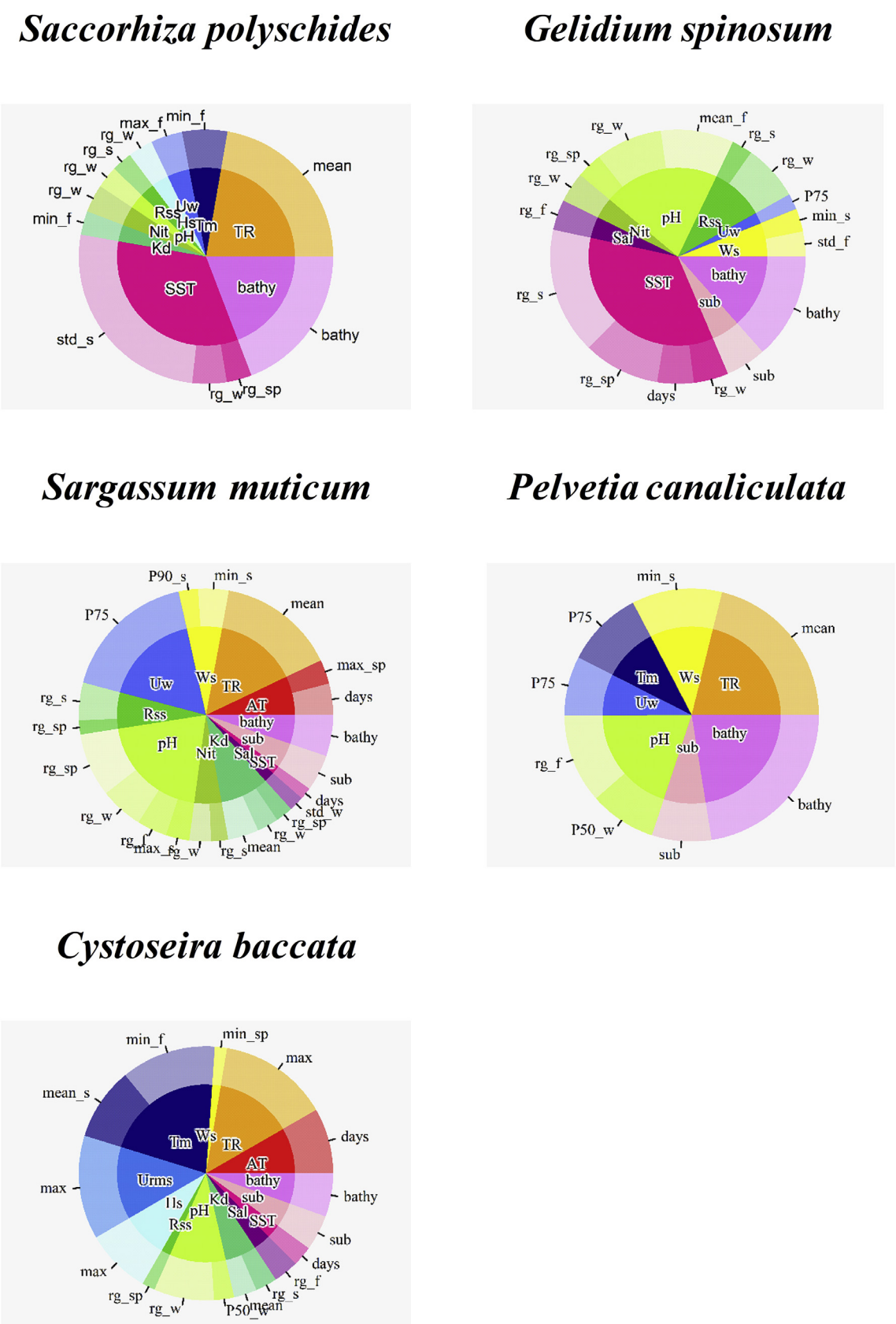

Fig. 3. Predictors contribution by species. Inner circles represent the variables and external subdivisions their parameters.

in both temperatures, but coping better with high SST values than with AT ones (Belsher, 1989). However, model also captured its preference by shallow waters and rocky substrates (Thomsen et al., 2006). Reproduction occurs in spring and summer, reason why the variability in the light availability during these seasons were included in the model. As a consequence of its invasive condition it is probably not in

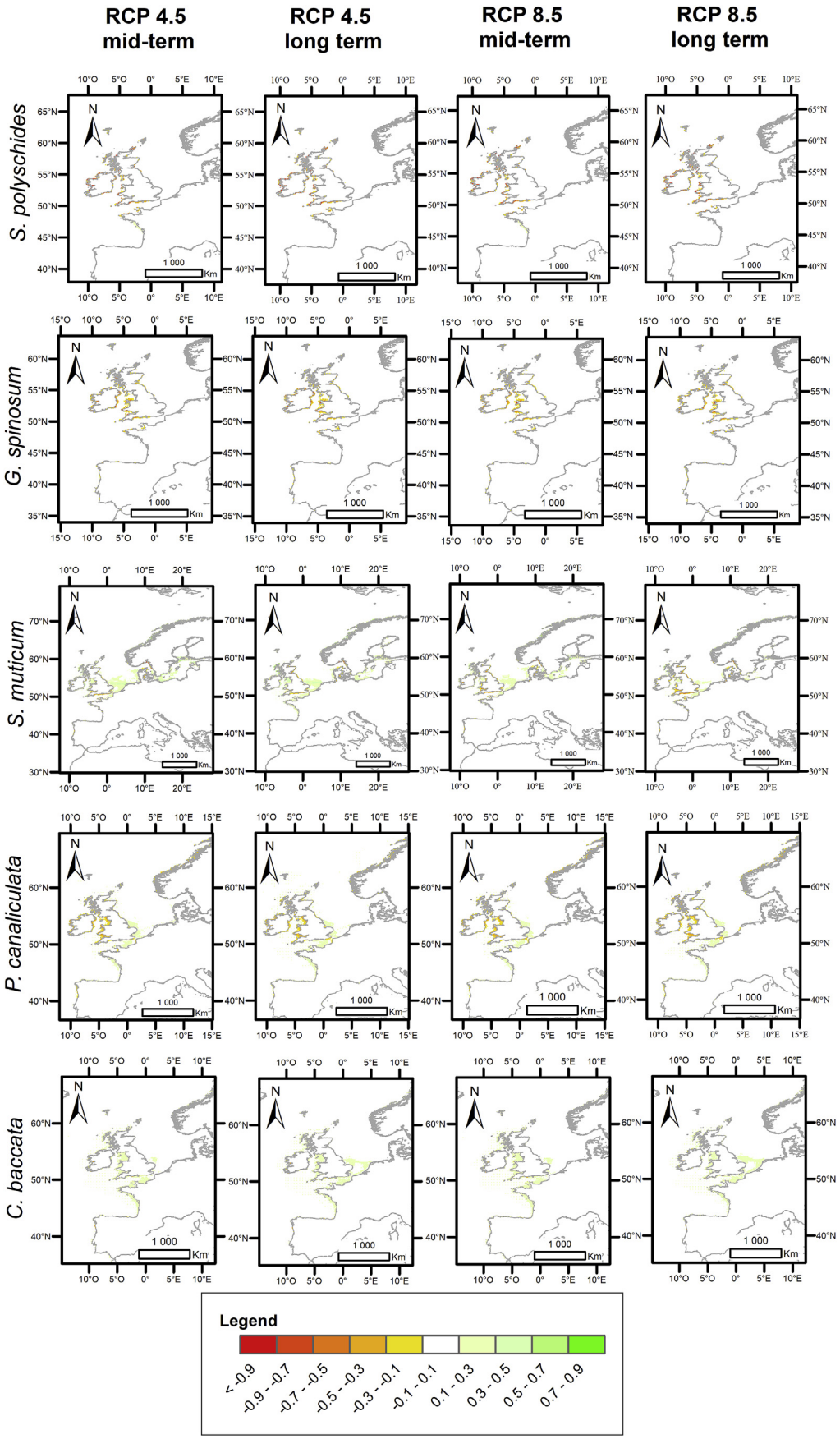

Fig. 4. Differences in the probability of presence predicted by the weighted ensemble of predictions (RCP 4.5 and 8.5 in the mid and long term) and historical period. Positive values (in green) indicate gains in the RCPs; meanwhile negative values (in red) represent losses. Note maps have been zoomed to the areas where values were different to zero to facilitate the visualization. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

equilibrium with the environment (Araújo and Pearson, 2005) and many variables influence its distribution. As SDMs assume this balance and the model was calibrated with data of the invaded range only, results must be considered carefully. Bearing this in mind, results agreed with existing knowledge, which suggests that model worked well. Historical distribution had captured the existing invaded areas, except the Mediterranean coasts of France (Critchley et al., 1990). No occurrence points were available in the Mediterranean for the analysis, which could be the reason of the underprediction in this area. Under climate change, model predicted a range expansion northward and an increase in its probability of occurrence. This trend continues the one already observed since its introduction in Europe (Engelen et al., 2015; Karlsson and Loo, 1999; Sánchez et al., 2005; Stæhr et al., 2000; Yesson et al., 2015).

P. canaliculata tolerates a wide range of exposure conditions (Lüning et al., 1990), reason why wind speed and bathymetry had an important weight in the model and it could bear with a high range of TR. The final model incorporated both terrestrial and marine variables, as models of other authors (Neiva et al., 2014). This fucoid is widely distributed in Europe and projections showed a decrease in its probability of occurrence, but some sites might be stable This could be the consequence of the high resilience that high intertidal species present (Harker et al., 1999; Skene, 2004). Besides, its probability increases in some areas, in agreement with the northward migration reported for the European Atlantic (Lamela-Silvarrey et al., 2012; Lima et al., 2007; Neiva et al., 2014; Piñeiro-Corbeira et al., 2016).

As *C. baccata* inhabits in a wide range of depth, exposure and sedimentation conditions (García-Fernández and Bárbara, 2016), its distribution was determined by terrestrial (TR, AT, Ws) and marine variables (SST, Urms, Tm, Hs). It is remarkable that most of the parameters selected for the model were the extreme ones, which highlighted its importance. Urms, Tm and Hs dependence plots supported the preference of *C. baccata* for sheltered areas, although it can tolerate semi-exposed conditions (Díez et al., 2003; Méndez-Sandín and Fernández, 2016). The model captured its southern distribution in the Atlantic (García-Fernández and Bárbara, 2016), whose limits increase in the RCP 8.5. Together with *S. muticum*, they were the only species that gained area. These results agreed with the changes detected in the north of Spain between 1977 and 2007, with a lengthened of *C. baccata* period of growth and an increase of its biomass (Méndez-Sandín and Fernández, 2016), suggesting a maintenance of this trend. As the model was constructed with a low number of records, it must therefore be interpreted cautiously, although results were in close agreement with previous studies.

For all species important changes in their range of distribution, which might modify the assemblage physical environment and the structure of the understory species. These shifts in species compositions have already been reported in the north of Spain (Díez et al., 2012; Fernandez, 2011; Voerman et al., 2013), which opens the gap of how biotic interactions would be modified and how the ecosystem services they provided would change.

In general, it can be said that the trend obtained in this work for kelps and fucoids is in agreement with other predictive models. The main trend is the disappearance of southern communities (Assis et al., 2018; Jüterbock, 2013; Wilson et al., 2019), which has been also detected in this study. However, meanwhile some fucoids are predicted to migrate northward, our models suggest a more dramatic scenario. That could be the consequence of including some hydrodynamic variables that are usually not considered and the methodological approach that selects the algorithms and their weights according to their ability to be transferable in time.

Modelled species distributional range shifts are subjected to a large number of uncertainties, such as the lack of biological records. In the context of this work, the scarcity of data in the Iberian Peninsula can affect the models, due to the importance of this area as distributional limit of algae (Ramos et al., 2016), therefore, results have to be interpreted with caution. Besides, in climate change context, distributional range shifts are the product of a multifactor complex interaction of abiotic and biotic conditions, dispersal potential and evolutionary capacity to adapt (Soberón and Peterson, 2005). Taking these aspects into account, the good accuracy of results obtained supports that this study constitutes the baseline for the identification of the species and locations potentially in threat. Additionally, the use of a broad pull of predictors provides a complete library of species tolerance thresholds, obtained in a cost-effective way, and very useful for researchers. It is remarkable the inclusion of hydrodynamic variables and extreme parameters, whose consideration as have been demonstrated of great significance.

5. Conclusions

Results presented in this work should be considered as a first step in the assessment of the magnitude of modelled range changes in seaweeds in Europe. Models built have been demonstrated a very good goodness-of-fit and discrimination performance, therefore it can be inferred that the most endangered species would be *S. polyschides* and *G. spinosum*, meanwhile *S. muticum* and *C. baccata* would be predicted to expand their range. *P. canaliculata* might decrease its probability of occurrence but it would be able to cope with changes.

Although requiring further development, the initial results presented here identified the species and areas at risk for five algae with different ecological requirements (from upper littoral to subtidal) and distributional patterns (native and invasive), therefore it can be used as surrogate for many others with similar ecological requirements. The novelty of this work is the supply to marine researchers and managers with the most complete pull until now of species physiological thresholds by the inclusion of hydrodynamic variables and extreme parameters, whose importance in species distributions has been demonstrated. It helps to fill the gap in knowledge between seaweeds ecology and environmental drivers on the one-hand and between science and managers on the other, by paying particular attention to building robust models with objective, reproducible, globally applicable and efficient methodology.

Authors' contributions

CH, ER, AP and JJ conceived the study and CH designed methodology. CH and ER acquired the data. CH analysed the data and led the writing. All authors contributed critically to the drafts and gave final approval for publication.

Declarations of interest

None.

Data accesssibility

The information is accessible at OCLE database (http://ocle.ihcantabria.com) for download and preview.

Acknowledgements

This work was funded by the National Plan for Research in Science and Technological Innovation from the Spanish Government 2013-2016 (Ministry of Economy and Competitiveness) [grant number C3N project CTM2015-68244-R] and co-funded by the European Regional Development's funds (FEDER). Camino Fernández de la Hoz acknowledges financial support under a predoctoral grant from the Spanish Ministry of Economy, Industry and Competitiveness [grant number: BES-2016-076434]. This work is part of the PhD of Camino Fernández de la Hoz, under the supervision of Araceli Puente and José Antonio Juanes. The authors are grateful to J.M. Álvarez-Martínez for his

suggestions and comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2019.04.012.

References

Acuna, E., Rodriguez, C., 2004. A meta analysis study of outlier detection methods in classification. In: International IPSI 2004 Conference, Symposium on Challenges in Internet and Interdisciplinary Research. Mayaguez, Puerto Rico, pp. 25.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Álvarez-Martínez, J.M., Jiménez-Alfaro, B., Barquín, J., Ondiviela, B., Recio, M., Silió-Calzada, A., Juanes, J.A., 2018. Modelling the area of occupancy of habitat types with remote sensing. Methods Ecol. Evol. 9, 580–593. https://doi.org/10.1111/2041-210X.12925.

Araujo, M., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47. https://doi.org/10.1016/j.tree.2006.09.010.

Araújo, M.B., Pearson, R.G., 2005. Equilibrium of species' distributions with climate. Ecography 28, 693–695.

Araújo, R.M., Assis, J., Aguillar, R., Airoldi, L., Bárbara, I., Bartsch, I., Bekkby, T., Christie, H., Davoult, D., Derrien-Courtel, S., Fernandez, C., Fredriksen, S., Gevaert, F., Gundersen, H., Le Gal, A., Lévêque, L., Mieszkowska, N., Norderhaug, K.M., Oliveira, P., Puente, A., Rico, J.M., Rinde, E., Schubert, H., Strain, E.M., Valero, M., Viard, F., Sousa-Pinto, I., 2016. Status, trends and drivers of kelp forests in Europe: an expert assessment. Biodivers. Conserv. 25, 1319–1348. https://doi.org/10.1007/s10531-016-1141-7.

Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E., Rahbek, C., 2019. Standards for distribution models in biodiversity assessments. Sci. Adv. 5, 1–10. https://doi.org/10.1126/sciadv.aat4858.

Assis, J., Castilho Coelho, N., Alberto, F., Valero, M., Raimondi, P., Reed, D., Alvares Serrão, E., 2013. High and distinct range-edge genetic diversity despite local bottlenecks. PLoS One 8, 1–11. https://doi.org/10.1371/journal.pone.0068646.

Assis, J., Coelho, N.C., Lamy, T., Valero, M., Alberto, F., Serrão, E.Á., 2016. Deep reefs are climatic refugia for genetic diversity of marine forests. J. Biogeogr. 43, 833–844. https://doi.org/10.1111/jbi.12677.

Assis, J., Berecibar, E., Claro, B., Alberto, F., Reed, D., Raimondi, P., Serrão, E.A., 2017. Major shifts at the range edge of marine forests: the combined effects of climate changes and limited dispersal. Sci. Rep. 7, 1–10. https://doi.org/10.1038/srep44348.

Assis, J., Araújo, M.B., Serrão, E.A., 2018. Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. Glob. Chang. Biol. 24, e55–e66. https://doi.org/10.1111/gcb.13818.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Belsher, T., 1989. Sargassum muticum (Yendo) Fensholt sur le littoral français. Synthese des études 1983-1989. Plouzane, France.

Bosch, S., Tyberghein, L., Deneudt, K., Hernandez, F., De Clerck, O., 2017. In search of relevant predictors for marine species distribution modelling using the MarineSPEED benchmark dataset. Divers. Distrib. 24, 144–157. https://doi.org/10.1111/ddi.12668.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Model. 157, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4.

Breiman, L., 1984. Classification and Regression Trees. Routledge, New York.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Glob. Ecol. Biogeogr. 21, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x.

Broennimann, O., Di Cola, V., Petitpierre, B., Breiner, F., Scherrer, D., DAmen, M., Randin, C., Engler, R., Hordijk, W., Mod, H., Pottier, J., Di Febbraro, M., Pellissier, L., Pio, D., Mateo, R.G., Dubuis, A., Maiorano, L., Psomas, A., Ndiribe, C., Salamin, N., Zimmermann, N., Guisan, A., 2016. Ecospat: Spatial Ecology Miscellaneous Methods.

Burrows, M., Fox, C., Moore, P., Smale, D.A., Greenhill, L., Martino, S., 2018. Wild seaweed harvesting as a diversification opportunity for fishermen, Highlands and Islands Enterprise. https://doi.org/10.1007/s10811-011-9695-y.

Cavole, L., Demko, A., Diner, R., Giddings, A., Koester, I., Pagniello, C., Paulsen, M.-L., Ramirez-Valdez, A., Schwenck, S., Yen, N., Zill, M., Franks, P., 2016. Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. Oceanography 29. https://doi.org/10.5670/oceanog.2016.32.

Celis-Pla, P.S.M., Martinez, B., Korbee, N., Hall-Spencer, J.M., Figueroa, F.L., 2017. Ecophysiological responses to elevated CO2 and temperature in Cystoseira tamariscifolia (Phaeophyceae). Clim. Change 1–15. https://doi.org/10.1007/s10584-017-1943-y.

Cheminée, A., Sala, E., Pastor, J., Bodilis, P., Thiriet, P., Mangialajo, L., Cottalorda, J.M., Francour, P., 2013. Nursery value of Cystoseira forests for Mediterranean rocky reef fishes. J. Exp. Mar. Biol. Ecol. 442, 70–79. https://doi.org/10.1016/j.jembe.2013.02.003.

Coro, G., Magliozzi, C., Ellenbroek, A., Pagano, P., 2015. Improving data quality to build a robust distribution model for Architeuthis dux. Ecol. Model. 305, 29–39. https://doi.org/10.1016/j.ecolmodel.2015.03.011.

Critchley, A.T., Farnham, W.F., Yoshida, T., Norton, T.A., 1990. A bibliography of the invasive alga Sargassum muticum (Fucales: Sargassaceae). Bot. Mar. 33, 551–562.

de la Hoz, C.F., Ramos, E., Acevedo, A., Puente, A., Losada, íñigo J., Juanes, J.A., 2018a. Ocle: a European open access database on climate change effects on littoral and oceanic ecosystems. Prog. Oceanogr. 168, 222–231. https://doi.org/10.1016/j.pocean.2018.09.021.

de la Hoz, C.F., Ramos, E., Puente, A., Méndez, F.J., Menéndez, M., Juanes, J.A., Losada, I.J., 2018b. Ecological typologies of large areas. An application in the Mediterranean Sea. J. Environ. Manag. 205, 59–72. https://doi.org/10.1016/j.jenvman.2017.09.058.

Díez, I., Muguerza, N., Santolaria, a., Ganzedo, U., Gorostiaga, J.M., 2012. Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change. Estuar. Coast Shelf Sci. 99, 108–120. https://doi.org/10.1016/j.ecss.2011.12.027.

Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D., 2012. Climate change impacts on marine ecosystems. Ann. Rev. Mar. Sci. 4, 11–37. https://doi.org/10.1146/annurev-marine-041911-111611.

Duarte, C.M., Wu, J., Xiao, X., Bruhn, A., Krause-Jensen, D., 2017. Can seaweed farming play a role in climate change mitigation and adaptation? Front. Mar. Sci. 4. https://doi.org/10.3389/fmars.2017.00100.

Díez, I., Santolaria, A., Gorostiaga, J., 2003. The relationship of environmental factors to the structure and distribution of subtidal seaweed vegetation of the western Basque coast (N Spain). Estuar. Coast Shelf Sci. 56, 1041–1054. https://doi.org/10.1016/S0272-7714(02)00301-3.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.

Engelen, A.H., Serebryakova, A., Ang, P., Britton-Simmons, K., Mineur, F., Pedersen, M.F., Arenas, F., Fernández, C., Steen, H., Svenson, R., Pavia, H., Toth, G., Viard, F., Santos, R., 2015. Circumglobal invasion by the brown seaweed Sargassum muticum. Oceanogr. Mar. Biol. Annu. Rev. 53, 81–126. https://doi.org/10.1201/b18733-4.

Fernandez, C., 2011. The retreat of large brown seaweeds on the north coast of Spain: the case of Saccorhiza polyschides. Eur. J. Phycol. 46, 352–360. https://doi.org/10.1080/09670262.2011.617840.

Fralick, R.A., Baldwin, H.P., Neto, A.I., Hehre, E.J., 1990. Physiological responses of pterocladia and Gelidium (Gelidiales, Rhodophyta) from the Azores, Portugal. Hydrobiologia 204, 479–482.

Friedman, J.H., 1991. Multivariate adaptive regression splines. Ann. Stat. 19, 1–67. https://doi.org/10.1214/aos/1176347963.

Galván, C., Puente, A., Castanedo, S., Juanes, J.A., 2016. Average vs. extreme salinity conditions: do they equally affect the distribution of macroinvertebrates in estuarine environments? Limnol. Oceanogr. 61, 984–1000. https://doi.org/10.1002/lno.10267.

García-Fernández, A., Bárbara, I., 2016. Studies of the Cystoseira assemblages in northern Atlantic Iberia. An. del Jardín Botánico Madrid 73, 1–39. https://doi.org/10.3989/ajbm.2403.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under the receiver operating characteristic (ROC) curve. Radiology 143, 29–36.

Harker, M., Berkaloff, C., Lemoine, Y., 1999. Effects of high light and desiccation on the operation of the xanthophyll cycle in two marine brown algae. Eur. J. 37–41.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized additive models. Monogr. Stat. Appl. Probab. I, 352. https://doi.org/10.1016/j.csda.2010.05.004.

Hastie, T., Tibshirani, R., Buja, A., 1994. Flexible discriminant analysis by optimal scoring. J. Am. Stat. Assoc. 89, 1255–1270.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M., Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M., Figueira, W.F., Gilmour, J.P., Harrison, H.B., Heron, S.F., Hoey, A.S., Hobbs, J.P.A., Hoogenboom, M.O., Kennedy, E.V., Kuo, C.Y., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm, H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T., Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L., Wilson, S.K., 2017. Global warming and recurrent mass bleaching of corals. Nature 543, 373–377. https://doi.org/10.1038/nature21707.

IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (Geneva, Switzerland).

Jiménez-Alfaro, B., Suárez-Seoane, S., Chytrý, M., Hennekens, S.M., Willner, W., Hájek, M., Agrillo, E., Álvarez-Martínez, J.M., Bergamini, A., Brisse, H., Brunet, J., Casella, L., Dítě, D., Font, X., Gillet, F., Hájková, P., Jansen, F., Jandt, U., Kącki, Z., Lenoir, J., Rodwell, J.S., Schaminée, J.H.J., Sekulová, L., Šibík, J., Škvorc, Ž., Tsiripidis, I., 2018. Modelling the distribution and compositional variation of plant communities at the continental scale. Divers. Distrib. 24, 978–990. https://doi.org/10.1111/ddi.12736.

Jonsson, P.R., Kotta, J., Andersson, H.C., Herkül, K., Virtanen, E., Sandman, A.N., Johannesson, K., 2018. High climate velocity and population fragmentation may constrain climate-driven range shift of the key habitat former Fucus vesiculosus. Divers. Distrib. 24, 892–905. https://doi.org/10.1111/ddi.12733.

Josefsson, M., Jansson, K., 2011. NOBANIS - Invasive Alien Species. Fact Sheet Sargassum Muticum, Database of the European Network on Invasive Alien Species.

Jüterbock, A., 2013. Climate Change Impact on the Seaweed Fucus Serratus, a Key Foundational Species on North Atlantic Rocky Shores. Univ. Nord. University of Nordland.

Karlsson, J., Loo, L.O., 1999. On the distribution and continuous expansion of the Japanese seaweed - Sargassum muticum - in Sweden. Bot. Mar. 42, 285–294. https://doi.org/10.1515/BOT.1999.032.

Kohonen, T., 1998. The self-organizing map. Neurocomputing 21, 1–6. https://doi.org/10.1016/S0925-2312(98)00030-7.

Lamela-Silvarrey, C., Fernández, C., Anadón, R., Arrontes, J., 2012. Fucoid assemblages on the north coast of Spain: past and present (1977 - 2007). Bot. Mar. 55, 199–207. https://doi.org/10.1515/bot-2011-0081.

Lima, F.P., Wethey, D.S., 2012. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nat. Commun. 3, 1–13. https://doi.org/10.1038/ncomms1713.

Lima, F.P., Ribeiro, P.A., Queiroz, N., Hawkins, S.J., Santos, A.M., 2007. Do distributional shifts of northern and southern species of algae match the warming pattern? Glob. Chang. Biol. 13, 2592–2604. https://doi.org/10.1111/j.1365-2486.2007.01451.x.

Liquete, C., Cid, N., Lanzanova, D., Grizzetti, B., Reynaud, A., 2016. Perspectives on the link between ecosystem services and biodiversity: the assessment of the nursery function. Ecol. Indicat. 63, 249–257. https://doi.org/10.1016/j.ecolind.2015.11.058.

Lüning, K., Yarish, C., Kirkman, H., 1990. Seaweeds : Their Environment, Biogeography, and Ecophysiology. Wiley.

Marshall, N.A., Tobin, R.C., Marshall, P.A., Gooch, M., Hobday, A.J., 2013. Social vulnerability of marine resource users to extreme weather events. Ecosystems 16, 797–809. https://doi.org/10.1007/s10021-013-9651-6.

Martínez, B., Arenas, F., Rubal, M., Burgués, S., Esteban, R., García-Plazaola, I., Figueroa, F.L., Pereira, R., Saldaña, L., Sousa-Pinto, I., Trilla, A., Viejo, R.M., 2012. Physical factors driving intertidal macroalgae distribution: physiological stress of a dominant fucoid at its southern limit. Oecologia 170, 341–353. https://doi.org/10.1007/s00442-012-2324-x.

Martínez, B., Radford, B., Thomsen, M.S., Connell, S.D., Carreño, F., Bradshaw, C.J.A., Fordham, D.A., Russell, B.D., Gurgel, C.F.D., Wernberg, T., 2018. Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. Divers. Distrib. 24, 1350–1366. https://doi.org/10.1111/ddi.12767.

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, Monographs on Statistics and Applied Probability 37. Chapman and Hallhttps://doi.org/10.1016/0377-2217(84)90282-0.

Méndez-Sandín, M., Fernández, C., 2016. Changes in the structure and dynamics of marine assemblages dominated by Bifurcaria bifurcata and Cystoseira species over three decades (1977-2007). Estuar. Coast Shelf Sci. 175, 46–56. https://doi.org/10.1016/j.ecss.2016.03.015.

Montgomery, D.C., Peck, E.A., 1982. Introduction to Linear Regresssion Analysis. Wiley, New York.

Naimi, B., Araujo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modelling. Ecography 39, 1–8. https://doi.org/10.1111/ecog.01881. ver. 1.0–54.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37, 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x.

Neiva, J., Assis, J., Fernandes, F., Pearson, G.A., Serrão, E.A., 2014. Species distribution models and mitochondrial DNA phylogeography suggest an extensive biogeographical shift in the high-intertidal seaweed Pelvetia canaliculata. J. Biogeogr. 41, 1137–1148. https://doi.org/10.1111/jbi.12278.

Norton, T.A., 1977. Experiments on the factors influencing the geographical distribution of Saccorhiza polyschides and Saccorhiza dermatodea. New Phytol. 78, 625–635.

Norton, T.A., 1978. The factors influencing the distribution of *Saccorhiza polyschides* in the region of Lough Ine. J. Mar. Biol. Assoc. U. K. 58, 527. https://doi.org/10.1017/S0025315400028186.

Oliver, E.C.J., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L.V., Benthuysen, J.A., Feng, M., Sen Gupta, A., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Straub, S.C., Wernberg, T., 2018. Longer and more frequent marine heatwaves over the past century. Nat. Commun. 9, 1–12. https://doi.org/10.1038/s41467-018-03732-9.

Pace, M., Borg, J.A., Galdies, C., Malhotra, A., 2017. Influence of wave climate on architecture and landscape characteristics of Posidonia oceanica meadows. Mar. Ecol. 38, 1–14. https://doi.org/10.1111/maec.12387.

Pérez, J., Méndez, F.J., Menéndez, M., Losada, I.J., 2014. ESTELA: a method for evaluating the source and travel time of the wave energy reaching a local area. Ocean Dynam. https://doi.org/10.1007/s10236-014-0740-7.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175. https://doi.org/10.1111/j.2007.0906-7590.05203.x.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Piñeiro-Corbeira, C., Barreiro, R., Cremades, J., 2016. Decadal changes in the distribution of common intertidal seaweeds in Galicia (NW Iberia). Mar. Environ. Res. 113, 106–115. https://doi.org/10.1016/j.marenvres.2015.11.012.

Piñeiro-Corbeira, C., Barreiro, R., Cremades, J., Arenas, F., 2018. Seaweed assemblages under a climate change scenario: functional responses to temperature of eight intertidal seaweeds match recent abundance shifts. Sci. Rep. 8. https://doi.org/10.1038/s41598-018-31357-x.

Quintano, E., Celis-Plá, P.S.M., Martínez, B., Díez, I., Muguerza, N., Figueroa, F.L., Gorostiaga, J.M., 2019. Ecophysiological responses of a threatened red alga to increased irradiance in an in situ transplant experiment. Mar. Environ. Res. 0–1. https://doi.org/10.1016/j.marenvres.2019.01.008.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. Computing, R Foundation for Statistical, Vienna, Austria.

Ramos, E., Puente, A., Juanes, J.A., Neto, J.M., Pedersen, A., Bartsch, I., Scanlan, C., Wilkes, R., Van den Bergh, E., Ar Gall, E., Melo, R., 2014. Biological validation of physical coastal waters classification along the NE Atlantic region based on rocky macroalgae distribution. Estuar. Coast Shelf Sci. 147, 103–112. https://doi.org/10.1016/j.ecss.2014.05.036.

Ramos, E., Puente, A., Juanes, J.A., 2016. An ecological classification of rocky shores at a regional scale: a predictive tool for management of conservation values. Mar. Ecol. 37, 311–328. https://doi.org/10.1111/maec.12280.

Regos, A., Gagne, L., Alcaraz-Segura, D., Honrado, J.P., Domínguez, J., 2019. Effects of species traits and environmental predictors on performance and transferability of ecological niche models. Sci. Rep. 9, 1–14. https://doi.org/10.1038/s41598-019-40766-5.

Rico, J.M., 1992. Ecología, fisiología y cultivo de Gelidium latifolium (Grev.) Thur. et Born. de la región de Cabo Peñas (N de España).

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.C., Müller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinf. 12. https://doi.org/10.1186/1471-2105-12-77.

Rueness, J., Fredriksen, S., 1989. Field and culture studies of Gelidium latifolium (Grev.) Born. & Thur. (Rhodophyta) from Norway. Dep. Biol. Mar. Bot. 11, 177–185. https://doi.org/10.1080/00364827.1989.10413426.

Russo, D., Di Febbraro, M., Rebelo, H., Mucedda, M., Cistrone, L., Agnelli, P., De Pasquale, P.P., Martinoli, A., Scaravelli, D., Spilinga, C., Luciano, B., 2014. What story does geographic separation of insular bats tell? A case study on Sardinian rhinolophids. PLoS One 9. https://doi.org/10.1371/journal.pone.0110894.

Sánchez, Í., Fernández, C., Arrontes, J., 2005. Long-term changes in the structure of intertidal assemblages after invasion by Sargassum muticum (Phaeophyta). J. Phycol. 41, 942–949. https://doi.org/10.1111/j.1529-8817.2005.00122.x.

Sax, D.F., Early, R., Bellemare, J., 2013. Niche syndromes, species extinction risks, and management under climate change. Trends Ecol. Evol. 28, 517–523. https://doi.org/10.1016/j.tree.2013.05.010.

Schiel, D.R., 2006. Rivets or bolts? When single species count in the function of temperate rocky reef communities. J. Exp. Mar. Biol. Ecol. 338, 233–252. https://doi.org/10.1016/j.jembe.2006.06.023.

Schoener, T., 1989. Food webs from the small to the large: the Robert H. MacArthur award lecture. Ecology 70https://doi.org/10.2307/1938088. 1889–1589.

Seabra, R., Wethey, D.S., Lima, F.P., Campo, R., 2015. Understanding complex biogeographic responses to climate change. Sci. Rep. 5, 1–6. https://doi.org/10.1038/srep12930.

Skene, K.R., 2004. Key differences in photosynthetic characteristics of nine species of intertidal macroalgae are related to their position on the shore. Can. J. Bot. 82, 177–184. https://doi.org/10.1139/b03-148.

Smale, D.A., Wernberg, T., 2013. Extreme climatic event drives range contraction of a habitat-forming species. In: Proceedings of the Royal Society. Royal Society Publishing, pp. 1–9.

Soberón, J., Peterson, A.T., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers. Inf. 2, 1–10. https://doi.org/10.1093/wber/lhm022.

Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T., Krause-Jensen, D., 2000. Invasion of Sargassum muticum in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Mar. Ecol. Prog. Ser. 207, 79–88. https://doi.org/10.3354/meps207079.

Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science (80-.) 240, 1285–1293. https://doi.org/10.1126/science.3287615.

Tamburello, L., Bulleri, F., Balata, D., Benedetti-Cecchi, L., 2014. The role of overgrazing and anthropogenic disturbance in shaping spatial patterns of distribution of an invasive seaweed. J. Appl. Ecol. 51, 406–414. https://doi.org/10.1111/1365-2664.12199.

Thomsen, M.S., Wernberg, T., Stæhr, P.A., Pedersen, M.F., 2006. Spatio-temporal distribution patterns of the invasive macroalga Sargassum muticum within a Danish Sargassum-bed. Helgol. Mar. Res. 60, 50–58. https://doi.org/10.1007/s10152-005-0016-1.

Torresan, S., Critto, A., Rizzi, J., Zabeo, A., Furlan, E., Marcomini, A., 2016. DESYCO: a decision support system for the regional risk assessment of climate change impacts in coastal zones. Ocean Coast Manag. 120, 49–63. https://doi.org/10.1016/j.ocecoaman.2015.11.003.

Tuanmu, M.N., Viña, A., Roloff, G.J., Liu, W., Ouyang, Z., Zhang, H., Liu, J., 2011. Temporal transferability of wildlife habitat models: implications for habitat monitoring. J. Biogeogr. 38, 1510–1523. https://doi.org/10.1111/j.1365-2699.2011.02479.x.

Vapnik, V., 1995. The Nature of Statistical Learning Theory. Springer.

Vesanto, J., 1999. SOM-based data visualization methods. Intell. Data Anal. 3, 111–126. https://doi.org/10.1016/S1088-467X(99)00013-X.

Voerman, S.E., Llera, E., Rico, J.M., 2013. Climate driven changes in subtidal kelp forest communities in NW Spain. Mar. Environ. Res. 90, 119–127. https://doi.org/10.1016/j.marenvres.2013.06.006.

Vousdoukas, M.I., Velegrakis, a. F., Paul, M., Dimitriadis, C., Makrykosta, E., Koutsoubas, D., 2012. Field observations and modeling of wave attenuation over colonized beachrocks. Cont. Shelf Res. 48, 100–109. https://doi.org/10.1016/j.csr.2012.08.015.

Vranken, S., Bosch, S., Peña, V., Leliaert, F., Mineur, F., De Clerck, O., 2018. A risk assessment of aquarium trade introductions of seaweed in European waters. Biol. Invasions 20, 1171–1187. https://doi.org/10.1007/s10530-017-1618-7.

Warren, D.L., Seifert, S.N., 2010. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol. Appl. 21, 335–342. https://doi.org/10.1890/10-1171.1.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.

Werner, F.J., Graiff, A., Matthiessen, B., 2016. Temperature effects on seaweed-sustaining top-down control vary with season. Oecologia 180, 889–901. https://doi.org/10.1007/s00442-015-3489-x.

Wilson, K.L., Skinner, M.A., Lotze, H.K., 2019. Projected 21st-century distribution of canopy-forming seaweeds in the Northwest Atlantic with climate change. Divers. Distrib. https://doi.org/10.1111/ddi.12897.

Yesson, C., Bush, L.E., Davies, A.J., Maggs, C.A., Brodie, J., 2015. Large brown seaweeds of the British Isles: evidence of changes in abundance over four decades. Estuar. Coast Shelf Sci. 155, 1–9. https://doi.org/10.1016/j.ecss.2015.01.008.

Zhang, L., Liu, S., Sun, P., Wang, T., Wang, G., Zhang, X., Wang, L., 2015. Consensus forecasting of species distributions: the effects of niche model performance and niche properties. PLoS One 10, 1–18. https://doi.org/10.1371/journal.pone.0120056.